

RESEARCH ARTICLE

Influences of the area, shape and connectivity of coastal lakes on the taxonomic and functional diversity of fish communities in Southern Brazil

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<http://zoobank.org/1C679170-04D6-42B7-ADE7-A12AD8269243>

ABSTRACT. In this study we investigated the influence of landscape variables on the alpha taxonomic and functional diversity of fish communities in coastal lakes. We built an analytical framework that included possible causal connections among variables, which we analyzed using path analysis. We obtained landscape metrics for the area, shape and connectivity (estuary connectivity and primary connectivity to neighboring lakes) of 37 coastal lakes in the Tramandaí River Basin. We collected fish data from 49 species using standardized sampling with gillnets and obtained a set of traits related to dispersal abilities and food acquisition. The model that best explained the taxonomic diversity and functional richness took into account the shape of the lakes. Functional richness was also explained by estuary connectivity. Functional evenness and dispersion were not predicted by area or connectivity, but they were influenced by the abundant freshwater species. This indicates that all lakes support most of the regional functional diversity. The results highlight the importance of the dispersal process in this lake system and allow the conclusion that considering multiple diversity dimensions can aid the conservation of local and regional fish communities.

KEY WORDS. Alpha diversity, environmental filters, limiting similarity, neutral paradigm, geographic information system.

INTRODUCTION

Coastal lakes are spatially and temporally dynamic ecosystems containing a substantial quantity of biodiversity (Esteves et al. 2008, Petry et al. 2016). Even though in these systems many factors influence biological communities, most previous studies have focused on the importance of water quality in determining alpha diversity. From a regional perspective, the local climate (temperature, precipitation and wind patterns) is the main driver of water quality and nutrient availability, which influence taxonomic diversity (Heino et al. 2007, Caliman et al. 2010). Besides these regional factors, local biotic interactions and anthropogenic disturbances can modify taxonomic diversity (Esteves et al. 2008, Petry et al. 2016). Additionally, landscape characteristics (position, morphometry and connectivity) of the lakes may also determine community structure in lakes, although their use is very recent (Quinlan et al. 2003).

Aquatic biodiversity has many facets that can be quantified, including taxonomic and functional diversity (Villéger et al. 2017). Functional diversity results from the functional trait space occupied by the species that compose a community (functional richness), from the distribution of abundance within the functional trait space (functional evenness) and from the functional dissimilarity of species across the functional trait space (functional dispersion) (Mason et al. 2005, Villéger et al. 2008, Laliberté and Legendre 2010, Mouchet et al. 2010). Functional redundancy indicates a high overlap of functional groups across the functional trait space (Laliberté and Legendre 2010). In contrast, functional complementarity indicates low functional overlap and that each species in the community has unique traits (Villéger et al. 2008, Laliberté and Legendre 2010, Leitão et al. 2016). Splitting the three independent functional diversity facets (richness, evenness and dispersion) can provide insights into the strength of the impact of environmental or

biotic filters on community assembly (Mouchet et al. 2010, Leitão et al. 2016, Córdova-Tapia et al. 2017). Furthermore, incorporating the abundance of traits within the community may improve our understanding of functional diversity and community assembly, as some species may disproportionately occupy the functional space and, therefore, have a stronger effect on ecosystem functioning. The high abundance of some species may result from their tolerance to anthropogenic environmental changes (Villéger et al. 2008, Leitão et al. 2016).

The mechanisms that influence fish community diversity in lakes are mainly associated with the complexity of the area and the shoreline habitat (Tonn and Magnuson 1982, Eadie and Keast 2011, Petry et al. 2016), which are positively associated with primary productivity (Dodson et al. 2000), habitat heterogeneity (Dodson et al. 2009, Scheffer et al. 2006) and availability of refuges from large predators (Jennings et al. 1999). Particularly in coastal lakes, the salinity regimen is an important factor for fish communities at local and regional scales, in view of the changes it produces in species composition (Jones and West 2005, Pérez-Ruza et al. 2007, Camara et al. 2018). Regional dispersal can be an important determinant of alpha diversity, (Özkan et al. 2013, Spasojevic et al. 2014, Cardoso et al. 2017) since it is correlated with habitat isolation and landscape connectivity, which also affect fish species richness and composition (Olden et al. 2001, Bouvier et al. 2009, Guimarães et al. 2014). Connectivity, more than environmental heterogeneity, is directly linked to dispersal of organisms, which is one of the predominant mechanisms contributing to community diversity (Drakou et al. 2009). Recent studies have addressed the effects of landscape factors on the functional diversity of fish communities, mainly for lotic ecosystems (Pease et al. 2012, Dala-Corte et al. 2016, among others). For lakes, in general, the functional richness and evenness decrease with habitat isolation (Miyazono et al. 2010, Cheng et al. 2014).

The coastal lakes of Southern Brazil harbor a considerable proportion of the Neotropical fish diversity in fresh and brackish waters. These lakes are influenced by both marine and continental processes and were subjected to events of sea retraction and expansion, which connected and disconnected lakes during their formation (Schwarzbold and Schäfer 1984). Azevedo et al. (2017) compared distinct types of coastal ecosystems in Southeast Brazil and observed that coastal lakes supported more functionally distinctive fish assemblages than beaches and bays. In highly connected lakes, communities may become functionally homogenized due to the frequent movement of vagile species (Guimarães et al. 2014). Thus, the ecological complexity of lakes (e.g. marginal marshes, grasslands, coastal 'restingas' and rock outcrops) and the historical seawater retractions and expansions that shaped the coastal landscapes of Southern Brazil offer a rare opportunity to evaluate how landscape factors such as lake connectivity, area and shape determine patterns of functional diversity in fish communities (Mouillot 2007, Miyazono et al. 2010).

We quantified the relative importance of landscape metrics to the alpha taxonomic and functional diversity of

fish communities inhabiting lakes in the Tramandaí river basin in Southern Brazil. More specifically, we aimed to understand whether functional richness, evenness and dispersion are affected by lake characteristics (area and shape) and the connectivity of the lake with the surrounding lakes (primary connectivity) or the estuary zone (estuarine connectivity). For this, the causal relationships between these different variables were analyzed using a path analysis. We built an analytical framework that included all plausible causal connections between variables (Fig. 1). The effect of the area on taxonomic diversity is predicted to be mediated by how complex the shape of the lake is. Following to Tonn and Magnuson (1982), we assumed that the largest lakes are also the largest reservoirs of the species' pool in the system, therefore indicating the effect on both connectivity metrics. Assuming that functional diversity increases proportionally with taxonomic diversity (Mouillot et al. 2007), we predict that taxonomic diversity will have a positive effect on the functional richness, evenness and dispersion of fish communities (Villéger et al. 2010). Connectivity, mainly with the estuarine zone, should increase the effect of the area on taxonomic diversity by adding species from partially distinct habitats, increasing functional richness and dispersion in the lakes. On the other hand, the primary connectivity increases only the functional evenness, since it would facilitate and homogenize the effects of dispersal and abundance of the species.

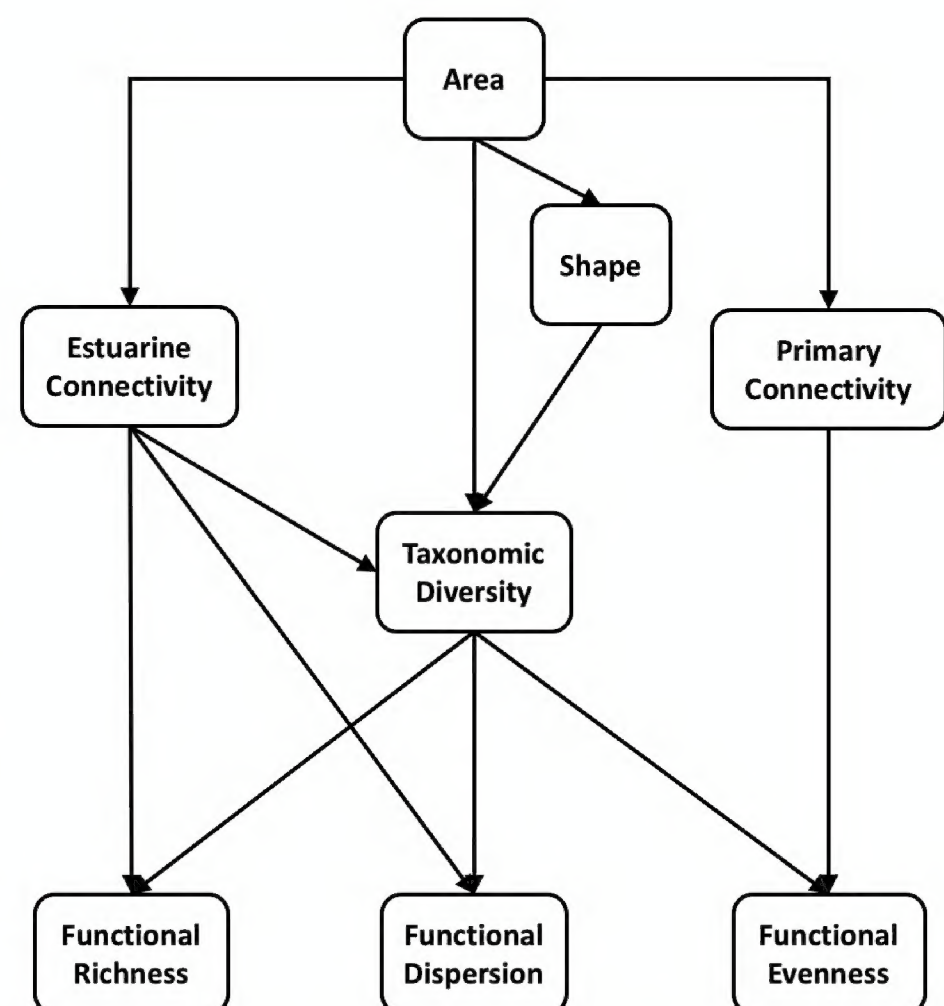


Figure 1. Hypothetical framework used to build the path model, with plausible causal connections between the landscape variables and both the taxonomic and functional diversity of the fish communities of the coastal lakes of the Tramandaí River Basin in Southern Brazil

MATERIAL AND METHODS

The Tramandaí River Basin (29°37'–30°30'S; 49°74'–50°24'W) is situated on the coast of the state of Rio Grande do Sul, Southern Brazil. It is a very representative coastal ecosystem containing 41 shallow coastal lakes formed recently in geological terms (Schwarzbold and Schäfer 1984), with varying degrees of interconnection and a single link to the ocean through the Tramandaí Estuary (see a map of the system in Guimarães et al. 2014). The formation of the system began in the Quaternary period through the deposition of sediments from marine transgressions and regressions, which produced sand barriers and isolated portions of water (Schwarzbold and Schäfer 1984). The region has a humid subtropical climate without a dry season (Hasenack and Ferraro 1989) and the mean temperature is 20 °C. February is the warmest month of the year.

We sampled 37 out of the 41 lakes from the river basin as it was not possible to access the other four lakes. The lakes have different degrees of connection between them, ranging from hydrologically isolated freshwater lakes to lakes that are directly connected to each other and/or to the estuary by channels. The estuary, which includes the Tramandaí Lagoon and its outlet channel to the sea, is a region of micro-tidal influence (Loitzenbauer and Mendes 2012) with seawater inflow and shorelines that flood during high tide. Consequently, three of the lakes have brackish waters (Würdig 1987).

Sampling in each lake consisted of the capture of fish using two sets of gillnets (in both the littoral and limnetic zone). Each gillnet set had an area of 180 square meters (mesh nodes of 15, 20, 25, 30, 35 and 40 mm) and was left for 24 hours in each lake. Samples were taken from May 2009 to April 2013. Since the activity periods of the species differ, we conducted between one and three sampling events in each lake per season (warm season, from October to April, and the cold season, from May to September). Larger lakes were sampled more often. The sampling effort was standardized by dividing the abundance

of each species by the number of sampling events in the lake, which ranged from two to six events.

Morphological functional traits of fish were chosen based on the work of Gatz (1979), Sibbing and Nagelkerke (2001), Dumay et al. (2004), Mouillot et al. (2007), Villéger et al. (2010, 2017) and Córdova-Tapia et al. (2017). Traits of the largest possible number of adults from each species were measured using an electronic caliper (precision of 0.1mm, Supplementary file S1). We measured morphological traits that represent mobility (capacity to swim and dispersal), food acquisition and behavior (the ability to use resources in the environment) (Table 1). For rare species whose presence in the lakes was known but no adult individuals were found, measurements were collected from individuals in scientific collections. Functional traits were calculated from the ratios between these morphological measurements (Table 1). Trait values were obtained for each species from the mean of their individual measurements as it was assumed that intraspecific variation is lower than interspecific variation (Villéger et al. 2012). In addition to the continuous morphological trait data taken from sampled individuals, other categorical trait data (caudal fin shape and trophic category) were taken from specialized literature (Rodrigues and Hartz 2001, Nunes and Hartz 2006, Malabarba et al. 2013) and from FishBase (<http://www.fishbase.de>, Froese and Pauly 2016). We obtained a set of 18 traits (6 continuous, 12 categorical/binary), but retained only those attributes represented by at least four species (16 traits: 6 quantitative, 10 binaries; Table 1). None of the traits had a Spearman correlation coefficient greater than |0.7|. Gower index was used to build the matrix of functional distances among fish species (Pavoine et al. 2009).

Lake attributes (Table 2) were estimated using GIS Idrisi Taiga (Eastman 2009) applied to a spatial database of the Tramandaí River Basin, which was produced from Landsat -TM images. The two connectivity indices (named estuarine, linking each lake with the estuarine zone and primary, linking each lake with the surrounding neighbor lakes, Table 2) were calculated using the

Table 1. Functional traits measured for fish species sampled from May 2009 to April 2013 in 37 coastal lakes of the Tramandaí River Basin.

Morphological traits measured (mm) or categorized	Functional trait	Ecological meaning	References
Standard length (Ls) Body depth (Bd)	Ratio of Ls/Bd	Hydrodynamic ability	Sibbing and Nagelkerke 2001
Length (Pl) and depth (Pd) of the pectoral fin	Ratio of Pl/Pd	Swimming ability, maneuverability at slow speeds and locomotion efficiency	Bellwood et al. 2002, Dumay et al. 2004
Length (Cl) and depth (Cd) of the caudal fin	Ratio of Cl/Cd	Decreases as the swimming ability of the fish declines; benthic species tend to have higher ratios whereas rapid swimmers have lower ratios	Dumay et al. 2004, Mouillot et al. 2007
Total length (Lt)	Lt maximum (Standardized by log (x+1) transformation)	Species with longer bodies are more successful over long distance dispersers than species of smaller sizes	Lucas and Baras 2001
Caudal fin shape	Cshape (forked, emarginate, rounded, truncated*, semilunar*)	Influence the forces exerted on the water	Lauder 2000
Eye diameter (D)	Ratio D/Lt	Detection of food and visual acuity	Piet 1998, Boyle and Horn 2006
Mouth depth (M)	Ratio M/Lt	Maximum size of the prey ingested	Sibbing and Nagelkerke 2001
Trophic Category	CT (invertivorous, planktophagous, piscivorous, omnivorous, benthophagous, detritivorous, insectivorous)	Position in the food web and feeding behavior	Gerking 1994

* Removed because the trait was not present in more than four species.

Table 2. Patch-level metrics for 37 coastal lakes of the Tramandaí River Basin. For more details see Guimarães et al. (2014).

Variable	Equation	Description
Area (A)		Calculated in hectares.
Shape (S)	$\text{Shape} = (0.282 \times \text{perimeter})/\sqrt{\text{area}}$	Corrected relationship between perimeter/area. Ranges from 1 (a perfect circle) to infinite (a long narrow shape, Farina 1998).
Primary Connectivity (PC)	$\text{PC}_i = \sum[(\text{RP})] \times [\log(\text{smallest CDis of the system}/\log_{10}(\text{CDis}_i))]$ $\text{RP} = \log(\text{Area}_i)/\log(\text{largest lake of the system})$	Related to recolonization potential (RP) and to the cost distance (Adriaensen et al. 2003, Guimarães et al. 2014). It considers the type of connection, lake area and the number and length of each connection. This index shows the degree of connection of each lake to its neighboring lakes. RP assumes that the largest lake is also the largest reservoir of the species pool in the system. Therefore, the larger the lake the greater its potential to contribute to the recolonization of nearby lakes (Tonn and Magnuson 1982).
Estuarine Connectivity (EC)	$\text{EC} = 1/\log(\text{CDis})$	Measure of functional connectivity based on the cost distance from each lake to the estuary, considering the friction value for each connection (Adriaensen et al. 2003, Guimarães et al. 2014).

concept of cost distance (CDis), which expresses the distance between two habitat patches weighted by the friction (resistance) imposed on the dispersal of an organism as it moves through a certain type of habitat (Adriaensen et al. 2003). Friction values were designated for each connection between lakes in the following way: rivers (friction = 3), channels (friction = 5) and small man-made channels (friction = 7). To measure the connectivity of the lakes connected to the estuary region, the other lakes were scored with a friction value of 1 to indicate that fish dispersal in these habitats is basically influenced by the distance they travel (Guimarães et al. 2014). None of the landscape covariates had a Spearman correlation coefficient greater than |0.7|.

Spatial autocorrelation may influence the patterns of functional similarity between assemblages (Devictor et al. 2010, Stuart-Smith et al. 2013), which may confound assessments of the trait-habitat relationship. To define the strength of the spatial autocorrelation on the functional patterns, we first calculated the mean pairwise functional distances between fish assemblages (Webb et al. 2008), which consist of the differences in species composition (Hellinger-transformed composition matrix, Legendre and Legendre 2012) weighted by the functional distance between species (based on the Gower distance according to the traits, Pavoine et al. 2009). The mean pairwise functional distance is a measure of functional beta diversity, which indicates the expected functional distance between two species randomly drawn from different communities (Webb et al. 2008). The functional beta diversity was calculated using the ‘comdist’ function of the picante package (R Core Team 2018). Then, we related the functional beta diversity to the spatial distances between lakes (Euclidean distance of Lat-Long coordinates) using a Co-Inertia analysis (Dolédec and Chessel 1994). Co-Inertia is a very general and flexible analysis as it allows us to relate two or more data sets that were composed using various distance measures and ordination methods. The Co-inertia analysis projects the position of points from two ordinations on to a common multivariate space, which was generated by an eigen-analysis of the cross-set covariance matrix (Dolédec and Chessel 1994, Legendre and Legendre 2012). We ran the Co-Inertia analysis using all the axes (i.e., the total variation from each dataset) of two different

Principal Component Analyses: one for the distances between lakes and the another for the functional distances between lakes (two and 36 ordination axes, respectively). Overlaps in the position of objects (lakes) from each data set across the common multivariate space indicate the overall consistency of the relationship between the spatial and functional distances. The RV coefficient measures the degree of consistency in the relationship between ordinations, like a correlation coefficient (Legendre and Legendre 2012). To evaluate the consistency of the co-structure of the spatial and functional distances between lakes, we applied the Monte-Carlo Permutation Test to the sum of the eigenvalues of the Co-Inertia analysis (RV coefficient \geq random RV coefficients, 999 permutations). This analysis was performed using the ‘ade4’ and ‘picante’ packages in the R environment (R Core Team 2018).

We used the complement of the Simpson Index (1-D) to access species taxonomic diversity (Magurran 2004) and three different functional indices (functional richness, functional evenness and functional dispersion) to access functional diversity (Villéger et al. 2008, Laliberté and Legendre 2010). We used different functional diversity components to evaluate the influence of lake area, size and connectivity on the overall functional space occupied by species (functional richness) and on how this space was occupied by fish species (functional evenness and dispersion). Functional richness, as measured by the FRic index, calculates the overall multivariate space occupied by coexistent species by linking the most extreme trait values, forming the vertices of a functional convex hull volume (Villéger et al. 2008). For this, we used nine PCoA axes (with 95% of total information retained). The number of PCoA axes was defined according to the number of species that was greater than the number of traits (“max” option in the ‘dbFD’ function, FD package, R Core Team 2018). The FRic index was standardized to obtain values between 0 and 1 (Laliberté et al. 2015). Functional evenness, as measured by the FEve index, represents the distribution of species abundance across the multivariate functional space (Villéger et al. 2008). Values will be low when some parts of the functional space are empty, while other parts are densely occupied. Neither FRic nor FEve estimate how species and abundance are spatially

dispersed, as they only measure the position of the species in the functional space (convex hull, Laliberté et al. 2015). Thus, we used the Functional Dispersion index (FDis), which calculates the mean distance of each species from the functional-space centroid (Laliberté and Legendre 2010). For the FDis calculation, the centroid and species dispersion values were weighted by species abundance, so that the position of the centroid would be near to the most abundant species. If the functional space contained rare species located close to the abundant ones, we would expect low FDis values (Laliberté and Legendre 2010). We run the FRic, FEve and FDis analyses using the function 'dbFD' from the FD package (R Core Team 2018).

We assessed the influence of lake area, shape and connectivity on fish-community diversity using a path analysis (Shipley 2000), following the analytical approach proposed by Brum et al. (2012). First, we built a theoretical path model with all the plausible causal connections, based on our hypothesis (Fig. 1). Next, we found the generalized linear models that best explained each of the endogenous variables in the path model (i.e. a variable that is caused some other variable in the path model) by using the model selection procedure based on Akaike's information criterion (AIC, Burnham and Anderson 2010). We selected the generalized linear model with the lowest AIC value. Since our dependent variables were of different types, we choose the appropriate error distribution for each type in the model selection procedure. We used the beta distribution in the model selection for FRic, FEve, taxonomic diversity and estuarine connectivity (proportion data from Ferrari and Cribari-Neto 2004) and gamma distribution in the model selection for FDis, shape and primary connectivity (continuous positive data from Zuur et al. 2009). The path coefficients of the constructed model were the β regression coefficients from the best previous models. In order to validate the entire path model, we employed Fisher's test for composite probabilities (Sokal and Rohlf 1994), called the C statistics by Shipley (2000). First, we compute the basis set by identifying the independence relationships between the variables in the path model (pairs of variables not connected by an arrow). For each independence test in the basis set, we evaluated the independence relationships by using partial correlation to control for the effects of all variables with direct ascendancy on both variables included in the independence relationship. Some of the variables in the path model presented correlated errors (CP and CE, FDis and FEve, FEve and FRic), and we could not establish a causal or unidirectional relationship between them. These relationships were incorporated to the path model by using a double-headed curve arrow between the variables, indicating the existence of correlated errors (Shipley 2000). The values on the double-headed curve arrows were the partial correlations after removing the effect of any covariates. After that, we computed the C statistics:

$$C = -2 \sum_{i=1}^k \ln P_i$$

where k is the number of independence relationships in the

basis set, P_i is the probability resulting from the partial multiple regression test for the independence relationship i. The C statistics follows a chi-square distribution with $2k$ degrees of freedom and the corresponding P value was used to validate the path model (Shipley 2000). The null hypothesis was that the independence relationships postulated in the model are valid, i.e. a P value below determined threshold would indicate that the independence assumptions of the basis set are false, and thus the model should be rejected. We used the 'stats' (R Core Team 2018) and 'betareg' (Cribari-Neto and Zeileis 2010) packages in R (R Core Team 2018) to run the model selection based on AIC and the partial correlations.

In addition to the direct causal effects (path coefficients) shown in the path model, we also computed the indirect effect and the total net effect of the predictors on the dependent variables in the model. The indirect effect was obtained from the product of the path coefficients of the sequence of arrows that lead from one variable to another (Shipley 2000). As we had more than one path connecting two variables, we obtained the overall indirect effect from all paths by summing all the indirect effects along all the paths between two variables. The net effect was then the sum of the direct and the overall indirect effect (Shipley 2000).

RESULTS

We captured a total of 7,870 individuals belonging to 49 fish species, 23 families and 9 orders (Supplementary file S1). The most frequent and abundant species (comprising more than 20% of the captured individuals) was *Cyphocharax voga* (Hensel, 1870) (Curimatidae) followed by *Geophagus brasiliensis* (Quoy and Gaimard, 1824) (Cichlidae) and *Oligosarcus jenynsii* (Günther, 1864) (Characidae). Functional richness ranged from 0.76 to 0.95 (mean \pm SD = 0.88 ± 0.05), functional evenness from 0.61 to 0.90 (0.75 ± 0.69), functional dispersion from 1.60 to 2.41 (1.93 ± 0.22) and taxonomic diversity (Simpson index) from 0.17 to 28.62 (6.41 ± 5.38). The Co-Inertia analysis revealed a lack of co-structure between the functional beta diversity and the spatial distances between lakes (RV coefficient = 0.172; $P = 0.124$; Supplementary file S2), indicating that there was no spatial autocorrelation in the data.

The final path model, representing the significant best model connecting the variables according to our hypothetical model, is presented in Fig. 2 ($C = 32.54$, $df = 36$, $P = 0.63$). It shows that the complexity of the shape of the lake was the only landscape variable that significantly and positively explained the observed patterns of taxonomic diversity. Taxonomic diversity had a positive effect on the functional richness, but not on functional evenness or dispersion. The only connectivity value positively associated with functional richness was estuarine connectivity. The indirect effects of landscape variables on the taxonomic and functional diversity were very small, and only the shape of the lakes had a positive influence on the functional richness (Table 3).

Table 3. The direct, indirect and net effect values of the lake area, shape and connectivity on the taxonomic and functional diversity of the fish communities in the coastal lakes of the Tramandaí River Basin in Southern Brazil, based on the final path model. TD = taxonomic diversity; CP = primary connectivity; CE = estuarine connectivity; FRic = functional richness; FEve = functional evenness; FDis = functional dispersion.

Predictor	Response	Direct	Indirect	Net
Area	Shape	-0.0400	0.0000	-0.0400
Area	TD	0.0000	-0.0064	-0.0064
Area	FRic	0.0000	-0.0052	-0.0052
Area	FEve	0.0000	0.0002	0.0002
Area	FDis	0.0000	0.0001	0.0001
Area	CP	0.1230	0.0000	0.1230
Shape	TD	0.1610	0.0000	0.1610
Shape	FRic	0.0000	0.1288	0.1288
Shape	FEve	0.0000	-0.0048	-0.0048
Shape	FDis	0.0000	-0.0032	-0.0032
CE	FRic	0.2370	0.0000	0.2370
TD	FRic	0.8000	0.0000	0.8000
TD	FEve	-0.0200	0.0000	-0.0200
TD	FDis	-0.0300	0.0000	-0.0300

DISCUSSION

The relationship between species richness and area has been established for a long time in ecology, particularly for freshwater ecosystems (Drakou et al. 2009, Petry et al. 2016). However, lake area was not the best predictor of taxonomic fish diversity in the Tramandaí River Basin. In our final model, area had a small negative influence on lake shape, indicating that larger lakes are less complex in form. Scheffer et al. (2006) discussed the small habitat size of shallow lakes and presented a framework suggesting that these lakes present a higher species richness than predicted by the classic island biogeography theory. In shallow lakes, the primary productivity occurs throughout the water column, resulting in greater biomass of macrophytes, adding resources and refuges to fish (Kruk et al. 2009). The lakes in the Tramandaí River Basin are shallow (mean maximum depth of around 3 m) and well connected (area had a positive influence on primary connectivity), allowing small lakes to support a high taxonomic diversity that is compatible with the diversity of larger lakes (lack of effect of area), in agreement with Scheffer et al. (2006).

The complexity of the shape of the lake had a direct positive influence on the taxonomic diversity and an indirect positive influence on the functional richness. This result may be related to the high proportion of different lake border habitats and the decreased available inner area (limnetic zone) of irregularly shaped lakes (i.e., lakes with higher shape index values, Farina 1998). The input of nutrients is favored in aquatic habitat patches with large perimeters (Pérez-Ruzafa et al. 2007), and therefore high productivity and availability of food resources

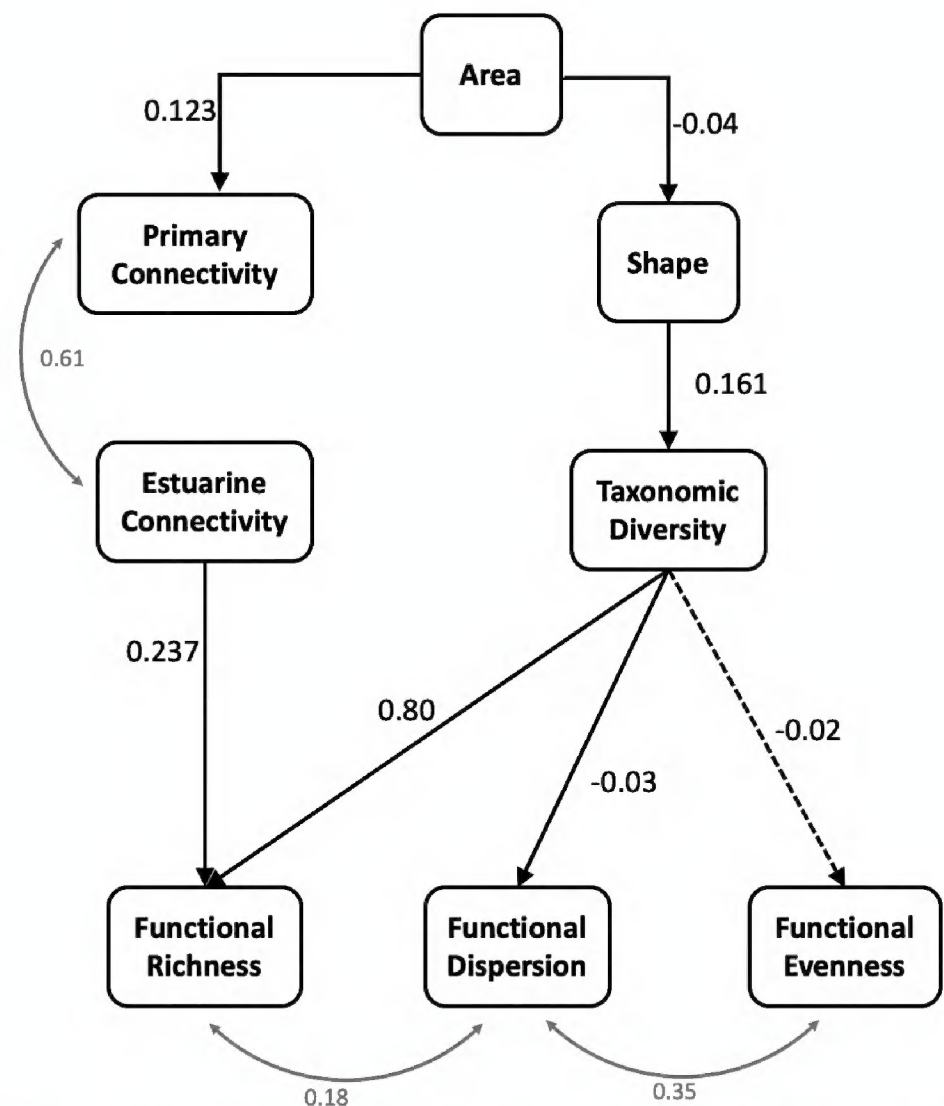


Figure 2. The final path model showing the causal relationships between the landscape variables and both the taxonomic and functional diversity of fish communities in the coastal lakes of the Tramandaí River Basin in Southern Brazil. Dotted line = not significant ($p > 0.05$). The curved double-headed arrows in grey depict correlated errors among variables.

would be expected. We only sampled fish communities with gillnets, which favor the capture of large species (Franco et al. 2012), even though the nets were placed in both the littoral and limnetic zones of the lakes. In the Tramandaí River Basin there are many small species (Lt max around 100 mm) living in the littoral zone (Malabarba et al. 2013) that were not detected by our sampling method. Despite of that, the effect of lake shape on functional richness was detected in our results. This reinforces the importance of the shape of the lake and consequently the importance of the littoral zones in shallow coastal lakes.

The positive association found in our study between taxonomic diversity and functional richness is not surprising because several other studies revealed a positive correlation between them (Pool et al. 2014, Carvalho and Tejerina-Garro 2015, among others). The volume of the functional space increases when functionally very distinct species are added in the community (Villéger et al. 2008). In our case, this occurred in the lakes near to the estuarine zone. Therefore, only the estuarine connectivity was important for (positively correlated to) functional richness in the Tramandaí River Basin, indicating that the lakes that are better connected with de estuarine zone have

different species' composition, with functionally distinct species. Salinity is one of the main factors influencing the distribution of fish species in coastal zones (Barletta et al. 2005, Mouillot et al. 2007, Pérez-Ruzafa et al. 2007, Sosa-López et al. 2007, Moura et al. 2012). Estuarine habitats allow for the occurrence of rare ecomorphologically distinct species such as the sole *Citharichthys macrops* Dresel, 1885 (higher value of the Ls/Bd) and the ladyfish *Elops saurus* Linnaeus, 1766 (higher value of the Pl/Pd). Guimarães et al. (2014) found that, in the same study area, lake connectivity was more important than lake area for estuarine species richness. In the Tramandaí River Basin three of the lakes studied have brackish waters (strictly coastal lagoons), despite the fact that these lakes are highly interconnected with other lakes. Azevedo et al. (2017) also found a higher functional diversity in coastal lagoons compared to bays or beaches (a consequence of the salinity gradient) on the Southeastern coast of Brazil. However, it is important to note that in their study the lagoons evaluated were not interconnected.

On the other hand, taxonomic diversity had a very small and negative influence on functional evenness and dispersion. Furthermore, no measure of connectivity was retained in our final model for both metrics. The results obtained showed that even when functional richness increased, FEve and FDis remained unaltered or even decreased. This result may be due to the effect of the more dominant functionally similar species sampled in the lakes. These metrics are heavily influenced by the most abundant and dominant species (Villéger et al. 2008, Laliberté and Legendre 2010) and, according to Hillebrand et al. (2008), the dominance reflects the distribution of traits in a community. In the Tramandaí River Basin the species with the greatest numbers of individuals were also present in almost all lakes (the characins *Cyphocharax voga* and *Oligosarcus jenynsii* and the cichlid *Geophagus brasiliensis*). We recalculated FEve and FDis metrics with only presence data of the species in the lakes and we obtained higher values significantly different for both metrics (Supplementary file S3), indicating the effect of the abundance of the dominant species.

Initially we may suppose that lakes seem to have sufficiently favorable environments to support the regional functional pool of traits related to dispersal and resource use, since the same dominant species are in all lakes. In natural systems organisms are subject to directional dispersal to find suitable environmental situations (Moritz et al. 2013). Even though it does not occur frequently, for some lake systems, other studies have found no evidence that fish species have dispersal limitations (Magnuson et al. 1998, Mason et al. 2007). The coastal lakes of the Tramandaí River Basin are shallow, which facilitates wind action (Cenzano and Würdig 2006). Wind is a major ecological force in this region, producing waves that resuspend bottom sediments (Schwarzbold and Schäfer 1984). This wind-driven resuspension of nutrients increases the efficiency of energy flow through the food chain, providing particulate organic matter to the lower trophic levels which consequently benefits the higher

trophic levels (Jeppesen et al. 1999). In general, shallow ponds and lakes have a greater tendency for eutrophication; however, the coastal lakes of the Tramandaí River Basin do not follow this pattern. The constant exposure to ocean winds produces both vertical and horizontal movements of the water, and since the lakes are shallow the sediment is well oxygenated, which means that there is a chemical fixation of phosphorus (Schäfer et al. 2013). This reduces the natural availability of this nutrient, decreasing the chances of eutrophication and preventing the oxygen reduction that these events generally cause (Schäfer et al. 2013). The efficiency of energy flow and the high levels of oxygenation make these lakes extremely productive ecosystems. This leads us to suppose that perhaps from a biological point of view, the lakes do not differ in their availability of resources.

Other environmental factors not measured on the lakes, like water quality and salinity (Schäfer 1992), could be important for FEve and FDis metrics since these variables influencing the local abundance of the species (Macedo-Soares et al. 2010, Souza et al. 2018). Similarly, if we had used other types of traits, such as habitat use, or traits related to life history strategies (Wine-miller 1989), maybe these functional metrics could have been explained by the landscape variables used. Particularly the traits linked with habitat use (Villéger et al. 2017) should be included in future studies, since they reflect the abundance of species with degradation of shoreline habitats in the lakes (Jennings et al. 1999, Villéger et al. 2010).

In addition, since the shape and connectivity (estuarine) positively influenced the functional richness, as previously discussed, both niche filtering and dispersal processes are involved for the functional diversity in the coastal lakes of the Tramandaí River Basin. As FEve and FDis were influenced by the most abundant and dispersal-prone species, these different processes could affect different groups of species (Pandit et al. 2009, Leitão et al. 2016): the more functionally original species would be influenced by niche processes, while the less functionally abundant species would be influenced by neutral processes. In our study, the most abundant and frequent species in the lakes are close in the functional space (Supplementary file S4). On the other hand, the most distinctive species are either estuarine or they belong to the loricariid family (the catfish *Loricariichthys anus* (Valenciennes, 1835) and *Rineloricaria quadrensis* Reis, 1983), a group that has low dispersal capacity (Pagotto et al. 2011, Rodrigues-Filho et al. 2018). Accordingly, the study about the dispersal capacity of the species becomes another important point for understanding the local dynamics of fish communities in this region.

The local diversity of a habitat patch is determined by dispersal, spatial dynamics and processes of extinction and colonization. In the coastal lakes of the Tramandaí River Basin, lake shape and estuarine connectivity were good predictors of the taxonomic diversity and functional richness of fish communities, but not of their functional evenness and dispersion. There was a certain level of functional redundancy, produced by

the spatially frequent and abundant species. Species coexistence could be explained by either niche and, for the traits analyzed, neutral dynamics. Coastal lakes are human-dominated ecosystems (Esteves et al. 2008) and according to our results, in terms of functional diversity conservation of fish (Mouillot 2007), it is important to maintain the diversity and the heterogeneity of the regional habitats among lakes to prevent biotic homogenization and to preserve the regional abundance of the species.

ACKNOWLEDGMENTS

We would like to thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the master scholarship to EAR, Phd scholarship to TFRG, postdoctoral fellowship to FTB, and PROEX program) and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, processes 304820/2014-8 and 483873/2007-1) for financial support. Additionally, we thank Ana Petry, João P. Vieira Sobrinho, Leandro Duarte, Luigi Naselli-Flores, David Hoeinghaus and the Subject Editor S. Adriano Melo and the anonymous reviewers for their valuable suggestions. We also extend special thanks to all the field assistants who made this research possible. All collection licenses (ICMBio – process 11174) and Ethics Committee approvals (UFRGS – process 15044) were obtained.

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Supplementary material 1

Supplementary file S1. Mean \pm S.E. of the functional traits for each fish species found in Tramandaí River basin.

Authors: Sandra M. Hartz, Elise A. Rocha, Fernanda T. Brum, André L. Luza, Taís de F.R. Guimarães, Fernando G. Becker.

Data type: species data.

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Link: <https://doi.org/10.3897/zoologia.36.e23539.suppl1>

Supplementary material 2

Supplementary file S2. The upper right-hand plot shows the position of the sites on the co-inertia axes using the functional dissimilarity (origins of the arrows) and spatial distances (arrowheads) between lakes.

Authors: Sandra M. Hartz, Elise A. Rocha, Fernanda T. Brum, André L. Luza, Taís de F.R. Guimarães, Fernando G. Becker.

Data type: species data.

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Link: <https://doi.org/10.3897/zoologia.36.e23539.suppl2>

Supplementary material 3

Supplementary File S3. Distribution of the observed values of the functional evenness (FEve) and dispersion (FDis) index calculated with species abundance and only with presence/absence records of fish communities of the coastal lakes of the Tramandaí River Basin.

Authors: Sandra M. Hartz, Elise A. Rocha, Fernanda T. Brum, André L. Luza, Taís de F.R. Guimarães, Fernando G. Becker.

Data type: species data.

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Link: <https://doi.org/10.3897/zoologia.36.e23539.suppl3>

Supplementary material 4

Supplementary File S4. Bidimensional chart from PCoA (Principal Coordinate Analysis) that represents the position between species described by the functional traits indicated in the Table 1.

Authors: Sandra M. Hartz, Elise A. Rocha, Fernanda T. Brum, André L. Luza, Taís de F.R. Guimarães, Fernando G. Becker.

Data type: species data.

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Link: <https://doi.org/10.3897/zoologia.36.e23539.suppl4>

Submitted: January 12, 2018

Accepted: November 27, 2018

Available online: June 27, 2019

Editorial responsibility: Adriano S. Melo

Author Contributions: SMH provided logistical support, guided and reviewed the research project and contributed to the writing of the paper; EAR conducted the fieldwork, obtained the traits fish data and contributed to the writing of the paper; ALL and FTB analyzed the data and contributed to the writing of the paper; TFRG and FGB conducted the field work and contributed to the logistical support.

Competing Interests: The authors have declared that no competing interests exist.

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